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FORUM

Criticism of the standard r-K dichotomy, with special reference to life histories of Diplopoda

Jean-François David

URA 689 C.N.R.S., Laboratoire d'Écologie générale, Museum national d'Histoire naturelle, 91800 Brunoy, France.

INTRODUCTION

For more than 20 years, the number of authors who have qualified populations as *r*-strategists or *K*-strategists on the basis of their life history traits has steadily increased. This has occurred until recently in studies on soil invertebrates (*e.g.* SATCHELL, 1980; MILLER & CAMERON, 1983; LÜFTENEGGER *et al.*, 1985; KARAMAOUNA, 1987; ATHIAS-BINCHE, 1989; VAN AMELSVOORT & USHER, 1989; IATROU & STAMOU, 1990; MA *et al.*, 1991). Although this terminology alludes to the *r*-selection and *K*-selection concepts of MACARTHUR & WILSON (1967), most authors refer, explicitly or implicitly, to the correlates of the two kinds of selection listed by PIANKA (1970, 1974). It is therefore assumed, in these *r-K* classifications, that a link has been established between the definitions of MACARTHUR & WILSON and the life history traits to which populations should evolve. In the present paper, it is argued that such a link is groundless. After a brief recall of the fitness definitions of MACARTHUR & WILSON, it will be pointed out that, within this framework, natural selection may lead to the life history traits listed by PIANKA as well as to the opposite. Some examples taken from soil invertebrates, mainly millipedes (Diplopoda), will show that life history evolution cannot be considered irrespective of a number of constraints which can be identified only by empirical knowledge of actual cases in the field.

The subject is not new and some of the arguments produced are borrowed from authors who have already warned against oversimplified classifications of traits using the *r-K* dichotomy (WILBUR *et al.*, 1974; STEARNS, 1977; BARBAULT & BLANDIN, 1980; PARRY, 1981; BOYCE, 1984; PARTRIDGE & HARVEY, 1988).

For clarity's sake, it is recalled that millipedes grow basically by anamorphosis, *i.e.* they hatch with a small number of rings (diplosegments) and, at each moult, they acquire new rings at the posterior end of the body. Maturity is achieved in a stadium which is either fixed or variable among individuals according to species. Age at first reproduction, between 1 and 4 years in most cases, also seems either fixed or variable among individuals according to species. A number of taxa are

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semelparous; others are iteroparous and usually breed once a year, adult body size continuing to increase between successive reproductions (undeterminate growth), up to about 10 years old in some species. As regards phylogeny, cladistic analyses have shown that ancestral millipedes were probably short forms, and that several periods of increase and decrease in the number of rings of adults (elongation vs. contraction) have occurred during evolution. Further details are given by Hopkin & Read (1992).

r AND K AS DEFINITIONS OF FITNESS

There are different conceptions of fitness, particularly if the evolution of populations and species is considered over long geological periods, during which the environment changes radically (*cf.* Dobzhansky, 1970; Cooper, 1984). But as regards evolutionary processes in the short term, an individual's fitness can be defined as its reproductive efficiency in a given environment. From the Darwinian viewpoint, the mean fitness of populations tends to increase by natural selection, at least for a number of generations after a genetic or environmental change, and provided no further change takes place. Obviously, it is taken for granted that the components of fitness can respond to selection, but examples show that they often respond in natural populations in spite of rather low heritabilities (*cf.* Hedrick, 1984).

In terms of population density, MacArthur (1962) and MacArthur & Wilson (1967) distinguished between two definitions of fitness in the short term. At low density, the intrinsic rate of increase, r_m (*), can measure fitness: then natural selection favours the genotypes which produce the most offspring capable of breeding per unit of time, and increases r_m. At high density, the same authors have advanced that K, the carrying capacity of the environment, is the best measure of fitness: when population density is regulated, natural selection favours the genotypes which are the most efficient in converting the available resources into offspring, and increases K.

It is useful to make two preliminary points regarding these definitions:

(i) Since r_m and K are measures of fitness, their variations stemming from genetic selection must not be confused with phenotypic differences without genetic components. Life history traits exhibit a great phenotypic plasticity and may respond to environmental factors (*e.g.* temperature, food quality, pollution). When no distinction can be made between variations due to genotypes and to the environment, one must be cautious in discussing life history evolution. As an example, it is unlikely that genetic differences can account for the variation in fecundity observed by Van Amelsvoort & Usher (1989) in Collembola reared on different food regimes; this fact should have prevented these authors from referring to r- and K-selection.

(ii) The K-selection concept, as stated by MacArthur & Wilson, implies that crowded populations evolve with an actual rate of increase $r_a = 0$ on account of limiting resources. The available resources allow only the replacement of

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(*) r_m refers to the maximum rate of increase under given environmental conditions, *i. e.* without negative effects of density and predation; when the latters occur, the actual rate of increase is termed r_a ($< r_m$).

populations, *i.e.* to maintain one female offspring per adult female, with a net replacement rate $R_0 = 1$. Other mechanisms not based on resources may determine K, such as predation or migration (Boyce, 1984), but they are not considered in the present paper.

Given the two definitions of fitness corresponding to evolution with or without crowding, Pianka (1970, 1974) made predictions about the life history traits to which populations should evolve in either case. According to his "correlates", selection increasing r_m would favour rapid development, early reproduction, small body size and semelparity. On the contrary, selection increasing K would favour slower development, delayed reproduction, larger body size and iteroparity. However, some considerations show that these correlates are by no means the only evolutionary possibilities that follow from the above definitions of fitness.

CRITICISM OF PIANKA's CORRELATES

The relationships between r_m, body size and generation time (T), are the main components of Pianka's (1970) reasoning. Two aspects are underlined: the strong positive correlation of body size and T, and, as a result, the strong inverse correlation of r_m with both body size and T. However, these relationships are significant only when viewing a wide range of organisms, from viruses to mammals; they become weaker when more limited taxa are considered, that is within definitions of fitness in the short term. In many invertebrates, for instance, generation time depends not only on the duration of body growth, but also on the duration of resting stages, which can last most of the year in highly seasonal environments (*e.g.* Crawford *et al.*, 1987). On the other hand, the relationships mentioned above completely overlook the positive correlation of body size and fecundity. As a rule, this relationship distinguishes poikilotherms from homeotherms (Reiss, 1989), and Sutton *et al.* (1984) have stressed its overriding importance for the evolution of life history traits in Isopoda. In Diplopoda, too, fecundity increases with female body size, not only in a given population (Heath *et al.*, 1974 for Glomerida; David, 1982 for Iulida; Couret & David, 1985 for Polyzoniida; Bhakat, 1989 for Polydesmida), but also between different populations of a species (Baker, 1984) and between closely related species with the same egg size (Blower & Gabbutt, 1964; Lewis, 1971; Blower & Miller, 1974). Of course, there are exceptions (*e.g.* Iatrou & Stamou, 1990), because factors other than body size influence fecundity. Moreover, not all the variations just mentioned have a genetic basis and an evolutionary significance. But, conversely, these variations show that selection for an increasing fecundity obviously involves an increase in body size in many Arthropoda. This must be kept in mind when considering the evolutionary possibilities of r_m and K being increased, for some of these possibilities do not correspond to Pianka's correlates.

Low density selection (*r*-selection)

With reference to the relation $r = \mathrm{Ln}\, R_0/T$ (where R_0 = net replacement rate, *i.e.* the sum of the product of the survival and fecundity value for each age class, and T = mean generation time), Pianka (1970) states that variations in R_0 alter r only slightly compared to changes in T. Accordingly, his first correlates are *rapid development* and *early reproduction* as ways of increasing r_m. However, even accepting this purely mathematical logic, an examination of the properties of the relationship between r, R_0 and T shows that (i) an increase in R_0, T being constant, can increase fitness provided R_0 is not too high; (ii) an increase in R_0 remains effective even though it implies an increase in T, provided the rising value $R'_0 > R_0^{(T'/T)}$ (fig. 1). These different mathematical options may correspond to biological facts.

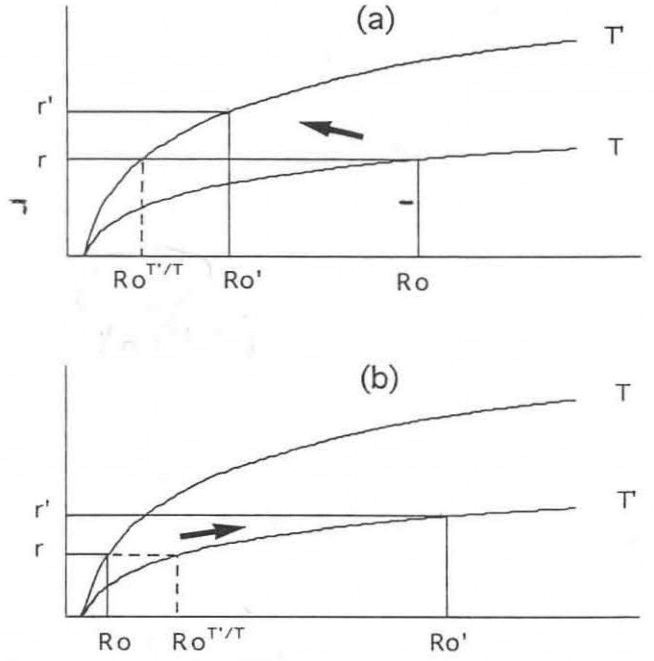

FIG. 1. – Plots of r against R_0 for different T values, showing that the relation $r = \text{Ln}\, R_0/T$ opens several evolutionary options to increase r, even if R_0 and T are positively correlated. *a*: Evolution decreasing $T\,(T' < T)$ leads to a higher r value ($r' > r$) in spite of a simultaneous decrease in R_0 ($R'_0 < R_0$), provided $R'_0 > R_0^{T'/T}$. This option is consistent with Pianka's correlates. *b*: Evolution increasing R_0 ($R'_0 > R_0$) leads to a higher r value ($r' > r$) in spite of a simultaneous increase in T ($T' > T$), provided $R'_0 > R_0^{T'/T}$. This option runs counter to Pianka's correlates.

A gain in fitness (r_m) due to an increase in R_0 with T constant is easy to conceive for semelparous species in which all females breed at the same age; it can also occur in iteroparous species under certain assumptions. In this case, natural selection may first favour traits which improve survival in the course of development. They may be either morphological, physiological or behavioural adaptations; or else some phenotypic plasticity which enables survival in a wide range of environmental conditions. Natural selection may also favour traits which increase fecundity – and therefore body size in Arthropoda. Two processes are involved in millipedes, without the age and stadium for breeding being necessarily changed, thus without generation time and survival being necessarily affected: acquisition of more rings at each moult ("lengthwise evolution"), or acquisition of larger rings at each moult ("widthwise evolution"). An example suggestive of a possible lengthwise evolution is the variation in the number of rings added at each moult in populations of *Tachypodoiulus niger* living at different altitudes – variation which remains in common garden experiments, according to Sahli (1978). Lewis (1971) gave an example suggestive of a possible widthwise evolution: between two *Xanthodesmus* species from Nigeria with annual life-cycles and the same number of rings, in the species with larger rings breeding females have many more ovocytes. The two processes, acquisition of more rings and acquisition of larger rings, may occur independently, as suggested by Enghoff's (1982) analysis of body size in an insular swarm of congeneric species.

If a gain in fitness is due to an increase in R_0 at the cost of an increase in T (fig. 1b), a substantial increase in fecundity is necessary. It can result either from oviposition delayed up to a larger stadium and an older age, or from oviposition extended over larger stadia by acquiring iteroparity. Both iteroparity and semelparity are commonplace in iulidan millipedes, though in distinct species. In comparison with a semelparous iulid which breeds in a single season at the age of 2 years, an iteroparous iulid which moults after its first breeding season and breeds again the next year has a longer mean generation time (2 yr$<T'<$3 yr). Nevertheless, the acquisition of iteroparity can lead to a value $R'_0 > R_0^{(T'/T)}$ – *i.e.* to a gain in fitness – even taking into account additional mortality resulting from the further moult, and a trade-off between fecundity and survival if preparations for the further moult impose a reproductive cost at the first breeding (Sibly & Calow, 1986). The slopes of the regression lines between egg number and ring number worked out in Iulida (*e.g.* David, 1982) are steep enough to satisfy $R'_0 > R_0^{(T'/T)}$ when realistic figures are substituted for survival rates. In theory, the increase in R_0 makes up the loss all the more easily as the generation time is longer and the R_0 value smaller in semelparous conditions.

Obviously, the decrease in T put forward by Pianka is also possible. In millipedes, it corresponds to different evolutionary processes such as faster stadial succession (decrease in T with R_0 constant) and maturation at a smaller stadium (decrease in T at the cost of a decrease in R_0 – fig. 1a), which Brolemann (1921) put together under the term *tachygenesis*. In fact, phylogenetic, biological and environmental constraints direct evolution either to a decrease in T or to an increase in R_0.

The influence of phylogenetic constraints can be illustrated by the following example. In entire orders (Polydesmida, Craspedosomatida), maturity is achieved after a number of moults which is absolutely unvarying in each species. In these conditions, any genetic change improving the growth rate of individuals (*e.g.* inducing changes in feeding habits, food assimilation, moulting-site selection, etc.) makes the achievement of maturity earlier. In some cases (but not always – *cf.* below), that can lead to a decrease in T. By contrast, in other orders such as the Iulida, the number of moults up to maturity varies within a species, but the age at maturity is possibly fixed in some species (David, 1982; 1992). If so, any genetic change improving the growth rate of individuals leads to bigger adults in a given time – *i.e.* to an increase in R_0 if fecundity is positively correlated with female body size. To a large extent, the direction of evolution is conditioned by the taxonomic position of species.

The influence of biological constraints can be illustrated by the following examples, where two species which live in France in the same forest sites are compared (fig. 2). In *Polydesmus angustus* egg-laying and hatching take place in late spring; the young females which develop to stadium VII by autumn mature and reproduce the following spring, at 1 year old; the young females which develop only to stadium V by autumn cannot reach maturity the following spring and reproduce at 2 years old (Couret, 1985). If the period of growth was a little shorter in "slow" individuals, this could result in shortening their generation time by one year. In such a population, a decrease in T may be favoured – unless the two T values are maintained by bet-hedging (Seger & Brockmann, 1987). On the contrary, *Melogona gallicum* is a truly annual species under normal weather conditions; egg-laying and hatching take place as early as the end of winter (David, 1984). In such a case, a decrease in T is much more difficult to achieve from a biological point of view, since it would imply an evolution towards polyvoltinism. An increase in R_0 instead seems a more direct way of increasing r_m.

Lastly, those constraints which arise from the biology of species also depend on the environment. In the same vein as above, a decrease in T which involves a change from univoltinism to polyvoltinism – a complicated process in the field, where seasonal conditions prevail – is made much easier where no seasonality occurs. For instance, the cosmopolitan species *Oxidus gracilis*, which inhabits hothouses in the temperate regions and can breed there at any time of the year, does show a generation time below one year (Causey, 1943). It is not known whether this trait results from adapted genotypes or whether it is a reversible mark of plasticity in the duration of stadia, which is common in Polydesmida (Snider, 1981); nevertheless, the case of *O. gracilis* illustrates how environmental changes influence the life cycle of some species and can completely transform the conditions of natural selection.

High density selection (*K*-selection)

First it must be pointed out that, in theory, evolution increasing r_m cannot be ruled out at high density in a crowded population where $r_a = 0$. This occurs if, all other things being equal, a new gene capable of increasing fecundity spreads into the population. The instantaneous death rate (d) increases to the same extent as the instantaneous birth rate (b), and $r_a = b - d$ remains zero, but selection nevertheless favours the most fecund genotypes, as diagrammatically shown by Lewontin (1978). If the population density drops thereafter so that $r_a = r_m$, it becomes evident that r_m has been increased.

However, in a crowded population, any genotype that makes possible a further rise in population density is favoured by selection (Lewontin, *ib.*), even though it leads at the same time to a substantial decrease in fecundity and therefore in r_m. In this respect, K is a measure of fitness characteristic of populations evolving at high density. K is the only measure to be taken into account for many authors who, in accordance with Gadgil & Bossert (1970), believe that selection acts reciprocally on the characters that determine r_m and K, depressing one when maximizing the other. But things may not be so simple, and experimental studies on species in which isogenic strains are available – which is far from being the case in millipedes

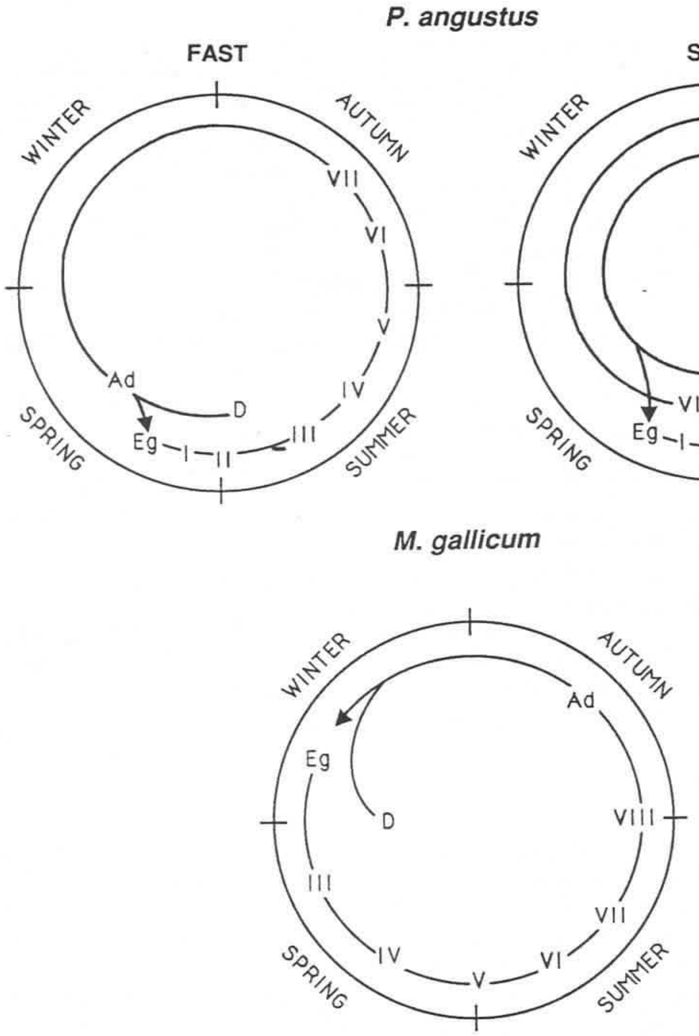

FIG. 2. – Simplified diagrams of the life cycles of two Diplopod species in the forest of Orleans (France). (Above) *Polydesmus angustus* shows a mixture of fast- and slow-growing individuals, with a mean generation time 1yr $< T <$ 2yr. (Below) *Melogona gallicum* is truly annual ($T =$ 1yr). The figures indicate the appearance of the different stadia. (Eg: Eggs; Ad: Adults; D: Death).

– have shown that the genotypes which give the highest r_m values also give the highest K values (LUCKINBILL, 1979; GIESEL & ZETTLER, 1980).

Nevertheless, suppose that a population evolving at high density actually increases K and not r_m. If the carrying capacity of the environment measures fitness, a limiting resource is available in such an amount that only one female offspring per adult female can be maintained. In these circumstances, K can increase only if genotypes "convert" an individual's share in resource into an amount adequate for more than one individual, with a higher equilibrium density ($K' > K$). This can result only from greater efficiency in the utilization of the limiting resource, in that the bearers of the new genotypes complete their life cycle with a lesser amount of resource. What biological processes can lead to that outcome? There are probably many of them, but it is not clear whether those changes in efficiency of resource utilization have a relationship with most life history traits (STEARNS, 1977). In any case, they do not all imply an increase in size – one of the correlates of K-selection according to PIANKA. It may be, for instance, more efficient assimilation of food which keeps constant the level of nutriments in the animal in spite of a lesser food intake; this enables an increase in population density but does not imply an increase in individuals' body size.

It can even be argued that evolution towards a reduced body size is a direct correlate of K-selection (BOYCE, 1984). In such a case, the available amount of resource may be shared between smaller individuals, with lower requirements in absolute values as regards food or space, provided that they remain able to ensure the replacement of the population ($R_0 = 1$). This at least leads to an increase in individual number, if not in biomass.

Conversely, an increase in body size is also possible within the framework of K-selection. For example, selection can favour such a process when food is a limiting factor if the variety of food sources shows a positive correlation with individuals' body size, as suggested in granivorous ants studied by DAVIDSON (1977). Again, the direction of evolution is determined by particular constraints, actual conditions, and not merely by the level of crowding of populations.

CONCLUSIONS

1. If one sticks to the primary conception of MACARTHUR & WILSON (1967) who distinguished between two definitions of fitness depending on whether populations were crowded or not (K or r_m), it is impossible to predict the evolution of life history traits. Evolutionary pathways are diverse enough for r-selection, in particular, to result in shorter or longer generation times, smaller or larger individuals, semelparous or iteroparous life cycles. In the Diplopoda, for instance, there is no reason why the processes of body elongation and contraction, which took place on several occasions in the course of evolution (DOHLE, 1988), should be regarded as K-selected or r-selected, respectively. If it is assumed that these processes were connected with increases in fitness, both of them could be regarded as having increased r_m: elongation is correlated with an increase in R_0, and contraction is correlated with a decrease in T.

Whether fitness is r_m or K, the life history traits which are evolved in each concrete case depend on a number of constraints peculiar to species and populations. They can be (i) phylogenetic (within a lineage, some traits respond to selection whereas others are thoroughly stable); (ii) biological (the evolution of a given trait must be compatible with species' biology); (iii) environmental (some features of the environment open or close the way to certain selective processes). PIANKA's (1970) correlates might be more a reflection of some constraints which he presupposed (variable or unpredictable environment and type III survivorship associated with r-selection; constant or predictable environment and type I or II survivorship associated with *K*-selection), than of crowding alone. However, this view, too, has been challenged on theoretical grounds (*e.g.* Schaffer, 1974), and there may be more than one adaptive solution to a particular environmental situation (Southwood, 1988).

2. Ecologists who are anxious to test the theory of MacArthur & Wilson about the shifts in fitness according to population density should use a more direct approach than the classification of life history traits. They should first measure r_m and K (or efficiency indices instead, such as growth efficiency, P/I, the ratio of production to energy intake), in specified conditions. The more r-selected of two populations is expected to show, above all, the higher r_m value, whatever process may have led to this result. As regards millipedes, there are few species for which laboratory data make it possible to calculate r_m and efficiency indices, and it is much the same for soil invertebrates in general. It would be advisable to develop such studies before speculating on the ecological significance of a hypothetical evolution increasing r_m or K.

However, even real differences in fitness value between populations would be insufficient for testing the theory. Furthermore, it would be necessary to know the whys and wherefores of these differences; to research whether they are a legacy from the past or whether they can be connected with present ecological conditions; and eventually to show that they depend on population density. Such an approach, which aims at producing a causal interpretation, may raise complex problems involving the whole population-environment system (Barbault, 1988); but it is more relevant than the simplistic *r-K* dichotomy.

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